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Seasonal variations in the response of soil CO_2 efflux to precipitation pulse under mild drought in a temperate oak (*Quercus variabilis*) forest

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ABSTRACT

Extreme precipitation events are predicted to increase in intensity and duration, with uncertain implications for terrestrial carbon (C) cycling. However, knowledge on the responses of soil CO_2 efflux to precipitation pulses in different seasons remains limited. Here we assessed the impacts of episodic precipitation pulses on soil respiration (SR) and its components [heterotrophic respiration (HR) and autotrophic respiration (AR)] under mild drought in different seasons in a temperate oak forest, Central China. Results showed that SR (24 h) increased with elevated precipitation levels, and the estimated precipitation-induced increases in the total amount of SR (3 months) in summer (17.86 g C m^{-2}) and autumn (13.57 g C m^{-2}) were greater than that in spring (9.73 g C m^{-2}) and winter (3.71 g C m^{-2}). Effects of precipitation pulse on HR and AR (24 h) varied with seasons, showing significant positive effects on HR in winter and AR in summer. Precipitation events significantly reduced the proportion of HR in SR in summer and autumn, but not in winter. Across all treatments, post-precipitation soil temperature, pre-precipitation soil moisture, and soil inorganic nitrogen are primarily responsible for the precipitation-induced increases in SR, whereas the stimulated HR after precipitation is largely depended on soil total porosity, pre-precipitation soil moisture, and microbial biomass C. Our study suggests that sporadic precipitation events have differential influences on SR and its components in different seasons. Our findings also emphasize that the importance of incorporating episodic extreme precipitation events and its influence on soil CO_2 efflux into the future predictions of forest C cycling under climate change.

1. Introduction

Soil respiration (SR), mostly consisting of heterotrophic respiration (HR) and autotrophic respiration (AR), is considered as a large part of carbon (C) efflux in forest ecosystem (Schlesinger and Andrews, 2000). Soil respiration and its components varied with seasonal changes in soil temperature, moisture, plant activity, and substrate availability (Davidson et al., 1998; Liu et al., 2016; Luan et al., 2012; Xie et al., 2014). Previous studies indicate that the changes in HR and AR differ in terms of how they respond to precipitation events of varying size (Huxman et al., 2004b). It has been reported that larger precipitation events are required to influence AR, mainly consisted of root and rhizosphere respiration (Shi et al., 2011). However, both large and small rainfall can initiate HR, which originated from the decomposition of soil organic matter, because substrate and microbes are always concentrated within the first few centimeters of topsoil (Cable et al., 2008). Numerous biological and ecological processes, such as fine root biomass and soil microbe activity always show a clearly expressed seasonal pattern (Liu et al., 2017). Therefore, the influences of precipitation events on SR and its components may differ between seasons, due to the temporal variations in biotic and abiotic factors (Wan et al., 2015). As a result, the contributions of HR and AR to SR may vary with precipitation intensities in different seasons. To develop long-term C cycle models and their coupling with the changing precipitation patterns, it is critical to understand the seasonal differences in the responses of SR and its components to episodic precipitation events.

The pulse of soil CO_2 efflux following wetting of dry soils (often called "Birch effect") (Birch, 1964; Jager and Bruins, 1975) has been recognized in arid desert ecosystem (Li et al., 2018; Ma et al., 2012a; Sponseller, 2007), semiarid grassland (López-Ballesteros et al., 2016; Rey et al., 2017; Yan et al., 2014), and savanna ecosystem (Fan et al., 2015). The discrete precipitation events induced increases in soil CO_2 efflux accounts for a substantial portion of annual soil CO_2 efflux (Smith et al., 2017; Song et al., 2016), which may have a large impact on soil C

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stocks in terrestrial ecosystems. The precipitation-induced soil CO_2 efflux is associated with physical, chemical, and biological mechanisms (Li et al., 2018; Unger et al., 2010). For example, the infiltration of rainwater may displace CO_2 that accumulated in soil pore spaces during dry periods (Huxman et al., 2004b). One chemical explanation for the stimulated respiration pulse after precipitation is that the pulses of CO_2 are originated from the microbial oxidation of labile soil organic matter, which becomes available as physically disrupt soil aggregates (Appel, 1998). Furthermore, the transient effects of precipitation event on soil CO_2 efflux have also been attributed to the increase in fungal and microbial biomass in response to water availability (Jager and Bruins, 1975; Unger et al., 2010). However, a complete understanding of the processes underlying the "Birch effect" has not been achieved. To date, our knowledge on the contributions of different environmental factors to the response of soil CO_2 efflux to precipitation events remains poor, especially for its seasonal variations.

Precipitation is the essential feature of climate change and a key element of the hydrological processes (Limsakul and Singhruck, 2016). Changing precipitation patterns has greatly affected climate stability, water availability, and ecosystem processes (Hao et al., 2017). Climate models project a general intensification of extreme precipitation events during the twenty-first century on continental to global spatial scales (Pfahl et al., 2017). Studies from observational data have shown that there is a positive trend in both the frequency and intensity of extreme precipitation events in Central China (Wang and Tian, 2010). In addition, extreme precipitation events show interannual and interdecadal variability. For example, Apr.-Jul. experienced an increasing trend of extreme precipitation events during the last 50 years in China, while Aug.-Sep. underwent a slightly decreasing trend (Fu et al., 2013). Therefore, a better understanding of how the extreme precipitation events in different seasons will influence soil CO_2 efflux is essential for predicting future terrestrial C feedbacks to climate change.

Forest ecosystems cover roughly one-third of the global land area and are vital sources and sinks of C (Pan et al., 2011). As a widely distributed tree species across the world (Nixon, 2006), oak forest covers a total area of 15.5×10^6 ha (Fang et al., 1996) and stores 835.94 Tg vegetation C (22.4% of all forests) (Wang et al., 2001) in China. Thus, oak forests play an important role in regulating C cycling and regional climate change in China. The effects of precipitation events on soil CO_2 efflux in forest ecosystems are less well understood compared to those in arid and semiarid ecosystems. In addition, recent studies in forest ecosystems have addressed that discrete precipitation events could either stimulate (Brito et al., 2013; Liu et al., 2014) or suppress (Lado-Monserrat et al., 2014; Wang et al., 2012) soil CO_2 efflux, which probably result from the differences in climate, vegetation, and soil conditions. These contradictory results may lead to an inaccurate estimate of soil CO_2 efflux, further adding to the uncertainty of C cycling in forest ecosystems.

In this study, a simulated precipitation experiment was carried out to determine the effects of episodic precipitation events on SR and its components in different seasons in a temperate oak forest, Central China. Specifically, we tested 1) whether there were any significant seasonal variations in the effects of precipitation events on SR and its components, and 2) how environmental drivers regulate the responses of SR to discrete precipitation pulse in different seasons.

2. Materials and methods

2.1. Study site

The study was conducted at the Jigong Mountains National Nature Reserve (31°46′-31°50′N, 114°01′-114°06′), located at a transitional zone from subtropical climate to warm temperate climate zone. The altitude of the study site is 144 *a.s.l.*. The soil at the site is yellow-brown soil based on China classification (Haplic Luvisol, FAO classification). Mean annual precipitation is 1063 mm over the period of 1951–2014, with 66% occurring from May to September. Mean annual temperature, minimum temperature in January, and maximum temperature in July are 15.2 °C, 1.9 °C, and 33.6 °C, respectively (China Meteorological Data Sharing Service System, http: data.cma.gov.cn). The average frequency of different precipitation events in different seasons was shown in Table 1. The highest frequency of the precipitation event was < 5 mm, and all the precipitation event < 40 mm accounted for approximately 95% of total precipitation events in this study (Table 1).

Table 1
Average frequency of different precipitation intensity in different seasons in the past 23 years (1994–2016) in the study site.

Season	Month	Percentage of different precipitation intensity (%)				
		$P \leq 5$	$5 \leq P \leq 10$	$10 \leq P \leq 20$	$20 \leq P \leq 40$	$P \geq 40$
Spring	Mar.	61.6	14.7	16.4	5.1	2.3
	Apr.	54.4	20.2	13.5	6.7	5.2
	May	51.4	13.2	17.5	14.2	3.8
Summer	Jun.	48.2	13.0	13.0	13.0	13.0
	Jul.	49.6	14.0	14.8	9.6	12.0
	Aug.	55.4	13.5	13.1	8.5	9.6
Autumn	Sep.	64.7	14.7	10.1	6.4	4.1
	Oct.	56.1	19.8	13.4	9.1	1.6
	Nov.	66.7	13.7	13.1	5.4	1.2
Winter	Dec.	68.0	19.2	12.0	0.8	0.0
	Jan.	77.0	15.6	6.7	0.7	0.0
	Feb.	66.7	21.5	9.6	2.3	0.0

The vegetation is characterized by warm-temperate deciduous forest. The dominant tree species consist of *Quercus* spp., *Pinus tabuliformis* Carr., *Acer truncatum* Bunge., and *Cunninghamia lanceolata* (Lamb.) Hook. Woody shrubs include *Lindera glauca* (Sieb. et Zucc.) BI., *Vitex negundo* L., *Symplocos chinensis* (Lour.) Druce, and *Euonymus alatus* (Tunb.) Sieb. Understory herbaceous plants include *Eriophorum comosum* Nees, *Lygodium japonicum* (Tunb.) Sw., and *Corydalis edulis* Maxim. (Miao et al., 2018). The field experiment was setup in an oak forest (slope < 5°) dominated by *Q. variabilis*, which was approximately 40 years-old. Stand density and basal area were 1883.6 tree ha^{-1} and 46.3 $m^2\,ha^{-1}$. Mean diameter at breast height of the stand was 13.4 ± 4.8 cm.

2.2. Experimental design

A total of 36 1 m × 2 m plots were set up with a complete randomized block design [detail experimental design see Liu et al. (2019b)]. Three blocks of 20 m × 20 m area were randomly arranged in the oak forest. Each plot was assigned to one of 12 different treatments: three levels of drought intensity [mild drought (10 days), moderate drought (20 days), and severe drought (30 days)] were crossed with four levels of precipitation events (0 mm, 5 mm, 10 mm, and 20 mm) in a factorial design. The plots without water addition (0 mm) represented control treatment, which underwent the same drought manipulation with the other precipitation treatments during our experimental period. Both drought and precipitation pulse treatments were carried out once in spring (April-May), summer (July-August), autumn (October-November), and winter (December-January), respectively. Data under moderate drought (20 days) and severe drought (30 days) treatments were not included and analyzed in this study. The effects of precipitation pulse on SR under different drought intensities were discussed in our another paper (Liu et al., 2019b).

Each plot was separated into two 1 m × 1 m subplots. One subplot was randomly selected for the trenching treatment to estimate HR. Another subplot was kept intact to estimate SR. Trenches of 70 cm deep and 20 cm wide were excavated around the subplot for HR in September 2016. Double nylon net (100 meshes per inch) was lined to prevent roots from penetrating in, and meanwhile allow lateral transfers of water and solution (Wei et al., 2015). The trenched subplots

were kept free of seedlings and herbaceous plant by periodical manual removal across the experiment.

The mild drought was simulated by excluding all the throughfall using rain shelters for 10 days in each season in 2017. Rain shelters similar to the design of Yahdjian and Sala (2002) were setup on all drought plots on 20 April, 9 July, 18 October, and 19 December after an effective precipitation (12.4 mm on 19 April, 10.3 mm on 8 July, 9.8 mm on 17 October, and 7.7 mm on 18 December). Water intercepted by the shelters during rain events was transferred into storage tanks and prepared for later precipitation simulation.

Precipitation events were simulated by spraying a known amount of water evenly. Following drought treatment in each season (30 April, 19 July, 28 October, and 29 December), four plots under mild drought treatment in each block were randomly selected and assigned four precipitation pulse events (0, 5, 10, and 20 mm within 10 min).

2.3. Soil CO_2 efflux, soil temperature, and moisture

A polyvinyl chloride (PVC) collar with 11 cm in diameter and 5 cm in height was inserted 2 cm into the soil in the center of each subplot for soil CO_2 efflux measurement. Soil CO_2 efflux was measured before, right after (0 min), and after 5 min, 10 min, 20 min, 30 min, 60 min, 180 min, 360 min, and 1440 min of the precipitation addition using the Soil CO_2 Flux System (LI-8100, Lincoln, Nebraska, USA). Soil temperature at 0–5 cm of the subplot for SR (ST_{SR}) and HR (ST_{HR}) was investigated using a soil thermistor connected to LI-8100. Soil volumetric water content (v/v%) at 0–5 cm depth of the subplot for SR (SM_{SR}) and HR (SM_{HR}) was measured using Time Domain Reflectometry (TDR 2000) soil moisture probe (Spectrum Technologies Inc. Plainfield; IL, USA). Soil temperature and moisture were investigated when each soil CO_2 efflux measurement was taken.

2.4. Fine root biomass

To examine the effects of fine root biomass (FRB) and soil physicochemical property on the response of soil CO_2 efflux to precipitation pulses, soil samples were collected after measurements of soil CO_2 efflux in each season. We collected soils with a hand auger (internal diameter 5 cm) to a depth of 10 cm from two points in each subplot. The mixed soil samples were placed in plastic bags, labeled, and stored in a refrigerator (4 °C) in the field. In the laboratory, each soil sample was first sieved by 2 mm mesh, and fresh soil samples were collected for further physicochemical analysis. The remaining plant samples were washed and hand sorted to separate living roots from dead roots, stem materials and litter fractions based on distinct morphological criteria and color. We used ≤ 2 mm diameter threshold to define fine roots so that it would be comparable to other previous studies. Live fine root biomass was estimated after oven drying at 70 °C for 72 h.

2.5. Soil inorganic nitrogen and microbial biomass carbon

Fresh soil sample sieved by 2 mm mesh was used for soil inorganic nitrogen (SIN, mg kg^{-1}) (NH_4^+-N and NO_3–N) analysis. NH_4^+-N and NO_3–N were extracted by shaking 10 g of fresh soil sample with 50 mL 2 M KCl for 1 h. The extracted solutions were stored frozen until analysis for NH_4^+-N and NO_3–N on a Discrete Auto Analyzer (SmartChem 200, WestCo Scientific Instruments Inc., Italy).

Soil microbial biomass C (MBC, mg kg^{-1}) was estimated on a 15-g oven-dry equivalent of fresh soil sample by the chloroform-fumigation-extraction method described by (Vance et al., 1987). Briefly, the concentration of soil organic C of the extracted solution was determined by a C analyzer (Vario TOC, German Elementar Company, Hanau, Germany) after acidification with one drop of 2 M HCl to remove any dissolved carbonate. The value of MBC was calculated as follows:

$$MBC = E_C/k_{EC}$$

Where E_C = (organic C extracted from fumigated soil) - (organic C extracted from non-fumigated soil) and k_{EC} = 0.45, which is the proportionality factor to convent E_C to MBC (Wu et al., 1990).

2.6. Soil bulk density and total porosity

Soil bulk density (BD) of 0–10 cm was measured using a stainless steel cutting ring, 5 cm in diameter and 5 cm in height (three replicates for each subplot) to collect a known volume of undisturbed soil. The dry mass was measured after oven-drying at 105 °C and the BD was calculated. Total soil porosity (TP) was calculated using Eq. (1) based on the BD and assuming a soil particle density of 2.65 g cm^{-3}.

$$TP = (1 - BD/PD) \times 100 \quad (1)$$

where TP is the total soil porosity (%), BD is the soil bulk density (g cm^{-3}), and PD is the soil particle density (g cm^{-3}).

2.7. Data analysis

Daily cumulative soil CO_2 efflux (g C m^{-2}) after each precipitation event during the experimental period (24 h) through SR, HR, and AR was determined for each subplot from the area under curves relating CO_2 efflux rate to time. The response sensitivity (g C m^{-2} mm^{-1}) of SR and HR (RS_{SR} and RS_{HR}) under different precipitation events in each subplot was estimated by dividing the difference of soil CO_2 efflux between post-precipitation and pre-precipitation values (e. g. $SR_{post\text{-}precipitation}$ - $SR_{pre\text{-}precipitation}$) with corresponding precipitation levels (mm).

To assess the change of soil CO_2 efflux after precipitation pulse, we also calculated the relative peak values (%) of SR and HR (RP_{SR} and RP_{HR}) based on the differences between the peak CO_2 efflux and pre-precipitation CO_2 efflux [*e. g.* (SR_{peak} - $SR_{pre\text{-}precipitation}$)/$SR_{pre\text{-}precipitation}$ × 100].

A back-of-the-envelope estimation on the seasonal cumulative soil CO_2 efflux (3 months) (SC, g C m^{-2}) through different respiration components (SC_{SR}, SC_{HR}, and SC_{AR}) was conducted using the soil CO_2 efflux, number of different precipitation event, and days of each month based on the following equation.

$$SC = \sum_{m=1}^{3} R_{0m} \times D_m + \sum_{m=1}^{3} (R_{pm} - R_{0m}) \times N_{pm} \quad (2)$$

where *SC* means seasonal cumulative soil CO_2 efflux during 3 months under different precipitation event; *R* means cumulative soil CO_2 efflux of SR, HR, and AR after each precipitation event during the experimental period (24 h); *D* means days in each month; *N* means the number of each precipitation event in each month; 0 means 0 mm precipitation; *m* (month) = 1, 2, and 3; *p* (precipitation) = 5, 10, and 20.

Two-way ANOVAs were used to analyze the main and interactive effects of season (S) and precipitation event (P) on ST_{SR}, ST_{HR}, SM_{SR}, SM_{HR} before and after precipitation events, and SR, HR, and AR, and the response sensitivity and relative peak value of SR and HR, and the proportion of HR in SR (HR/SR). Given that the interactions between season and precipitation events, One-way ANOVA was further used to test the effects of precipitation pulse on SR, HR, AR, HR/SR, response sensitivity, and relative peak values of SR and HR in each season. To determine the effects of environmental variables on soil CO_2 efflux after precipitation pulse in different seasons, stepwise multiple regressions were conducted, with SR and HR as the dependent variables, and ST, SM, FRB, MBC, SIN, BD, and TP as the independent variables. All statistical analyses were performed using the SPSS 13.0 software package for Windows (SPSS Inc., Chicago, USA).

Table 2
Results (P values) of two-way ANOVA on the effects of season (S), precipitation event (P), and their interactions on pre- and post-precipitation soil temperature and moisture for soil respiration (SR)($PrST_{SR}$, $PoST_{SR}$, $PrSM_{SR}$, and $PoSM_{SR}$), heterotrophic respiration (HR) ($PrST_{HR}$, $PoST_{HR}$, $PrSM_{HR}$, and $PoSM_{HR}$), SR, HR, AR, and response sensitivity and relative peak value of SR and HR (RS_{SR}, RP_{SR}, RS_{HR}, RP_{HR}), and proportion of HR in SR (HR/SR) (n = 3). Bold numbers are statistically significant ($P <$ 0.05).

Variables	Season (S)	Precipitation (P)	S × P
$PrST_{SR}$	**0.000**	0.089	0.161
$PoST_{SR}$	**0.000**	0.231	0.826
$PrSM_{SR}$	**0.000**	0.707	0.241
$PoSM_{SR}$	**0.028**	**0.030**	**0.041**
$PrST_{HR}$	**0.000**	0.363	0.936
$PoST_{HR}$	**0.000**	0.595	0.862
$PrSM_{HR}$	**0.000**	0.341	0.701
$PoSM_{HR}$	**0.008**	**0.032**	**0.044**
SR	**0.000**	**0.030**	0.392
HR	**0.000**	0.321	**0.042**
AR	**0.001**	**0.005**	**0.034**
HR/SR	**0.001**	0.140	0.086
RS_{SR}	**0.000**	**0.000**	**0.002**
RP_{SR}	**0.000**	0.060	**0.001**
RS_{HR}	**0.000**	**0.000**	**0.004**
RP_{HR}	**0.000**	0.168	**0.006**

3. Results

3.1. Soil temperature and moisture

There were strong seasonal fluctuations in pre- and post-precipitation ST_{SR} and ST_{HR} (all $P <$ 0.05, Table 2), showing the highest values (25.3–26.9 °C) in summer and lowest ones (7.9–10.5 °C) in winter (Fig. 1a and d). However, no effects of precipitation pulse or its interactions with season were observed on pre- and post-precipitation ST_{SR} and ST_{HR} (all $P >$ 0.05, Table 2).

Both SM_{SR} and SM_{HR} before precipitation showed remarkable seasonal fluctuations with the highest values in autumn (8.5–10.5% for SR) and summer (9.1–10.8% for HR), and the lowest values (4.3–6.3%) in winter (all $P <$ 0.05, Table 2, Fig. 2a and b). In each season, soil moisture before precipitation pulse showed no statistical differences among plots (all $P >$ 0.05, Table 2, Fig. 2a and b).

Both SM_{SR} and SM_{HR} after precipitation addition showed substantial seasonal variations (both $P <$ 0.05, Table 2), reaching maximum values in summer and minimum values in winter. Upon rewetting, soil moisture positively responded to precipitation levels ($P <$ 0.05, Table 2). Compared with control plots, precipitation events with 5 mm, 10 mm, and 20 mm significantly increased SM_{SR} by 2.19–5.40%, 3.63–8.14%, and 8.88–14.11%, and SM_{HR} by 0.69–6.22%, 4.07–8.06%, and 7.93–14.27%, respectively (Fig. 2c and d). In addition, the effects of precipitation addition on soil moisture varied with seasons ($P <$ 0.05, Table 2). Precipitation treatments resulted in higher increases in both SM_{SR} (5.40–14.11%) and SM_{HR} (6.22–14.27%) in summer, but lower increments in spring (2.19–8.88% for SM_{SR} and 0.69–7.93% for SM_{HR}) (Fig. 2).

3.2. Soil respiration

Soil respiration over the 24 h. period after precipitation events differed significantly between seasons ($P <$ 0.01) and precipitation levels ($P <$ 0.05, Table 2, Fig. A1a-d). Soil respiration under different precipitation levels ranged from 3.13 g C m^{-2} to 4.20 g C m^{-2} in summer, which was on average 78.8%, 184.3%, and 572.2% greater than those in spring, autumn, and winter, respectively ($P <$ 0.05, Fig. 3a). In spring, SR under 20 mm precipitation event was 40.8% greater than that in control plots ($P <$ 0.05, Fig. 3a). Precipitation events with 10 and 20 mm levels substantially increased SR by 28.2% and 34.5% in summer ($P <$ 0.05, Fig. 3a). In comparison with control plot, treatments with 5, 10, and 20 mm water additions significantly increased SR by 55.9%, 56.9%, and 33.1% in autumn, and by 44.7%, 36.5%, and 27.6% in winter, respectively (all $P <$ 0.05, Fig. 3a). The average increment of SR (24 h) caused by precipitation pulse in spring (23.5%) and summer (22.0%) was lower than that in autumn (48.6%) and winter (36.3%; Fig. 3a). In contrast, the increases in SC_{SR} across 3 months caused by precipitation in spring (18.73 g C m^{-2}) and summer (17.86 g C m^{-2}) were greater than that in autumn (13.57 g C m^{-2}) and winter (3.71 g C m^{-2}; Table 3). Additionally, SC_{SR} caused by episodic precipitation events was 53.87 g C m^{-2} yr^{-1}, which accounted for 9.4% of annual total soil CO_2 efflux (Table 3).

3.3. Heterotrophic respiration

Heterotrophic respiration significantly differed between seasons ($P <$ 0.01, Table 2, Fig. A1e-h), with higher values in summer (2.55–3.01 g C m^{-2}) and smaller ones in winter (0.39 – 0.56 g C m^{-2}) (Fig. 3b). The effects of precipitation events on HR varied with seasons ($P <$ 0.05, Table 2). Treatments with 5 and 10 mm precipitation significantly increased HR by 27.9% and 37.6% in spring, respectively ($P <$ 0.05, Fig. 3b). However, HR was not affected by precipitation events in summer. Precipitation event of 5 mm significantly enhanced HR by 22.3% in autumn. In winter, treatments with 5, 10, and 20 mm precipitation substantially increased HR by 42.3%, 33.0%, and 16.4%, respectively (Fig. 3b). Annual estimated precipitation-induced increase in SC_{HR} is 24.91 g C m^{-2}, accounting for 5.3% of annual total CO_2 efflux through HR (Table 3).

3.4. Autotrophic respiration

Similar to SR and HR, AR also showed substantial seasonal fluctuation ($P <$ 0.01, Table 2, Fig. A1i-l), with greater values in summer (0.57–1.19 g C m^{-2}) and lower values in winter (0.03 – 0.08 g C m^{-2}) (Fig. 3c). In addition, both precipitation treatment and its interaction with season showed significant effects on AR (both $P <$ 0.05, Table 2). In spring, only treatment with 20 mm precipitation addition showed a positive effect on AR (99.6%; Fig. 3c). Precipitation events with 5, 10, and 20 mm substantially elevated AR by 49.7%, 108.4%, and 107.6% in summer, respectively. Compared with the control plots, precipitation of 20 mm levels substantially increased AR in autumn (Fig. 3c). In winter, all precipitation events showed no impacts on AR. Annual estimated precipitation-induced increase in SC_{AR} is 28.96 g C m^{-2}, which is 27.5% of annual total CO_2 efflux through AR (Table 3).

3.5. Proportion of heterotrophic respiration in soil respiration

The values of HR/AR significantly differed between seasons, showing greater values (81.9–93.1%) in winter (Fig. 3d). In addition, the effects of precipitation treatment on the HR/SR varied with seasons (P < 0.05, Table 2). In spring, the HR/SR was elevated by 10.5% and 22.9%, under 5 and 10 mm events, respectively, but was reduced by 12.4% under 20 mm event (Fig. 3d). Moreover, all precipitation treatments (5, 10, and 20 mm) significantly reduced the values of HR/SR in both summer (8.6–11.6%) and autumn (12.6–18.9%) but showed no effects in winter (Fig. 3d).

3.6. Response sensitivities of SR and HR

The RS_{SR} and RS_{HR} varied with seasons (both $P <$ 0.01, Table 2), showing the greatest values in summer and the lowest values in winter (Fig. 4a and b). In addition, both RS_{SR} and RS_{HR} decreased significantly with elevated precipitation sizes (both $P <$ 0.01, Table 2). The effects of precipitation events on the RS_{SR} and RS_{HR} differed among seasons (both $P <$ 0.01, Table 2). The RS_{SR} and RS_{HR} showed significant differences among three precipitation treatments in both spring and

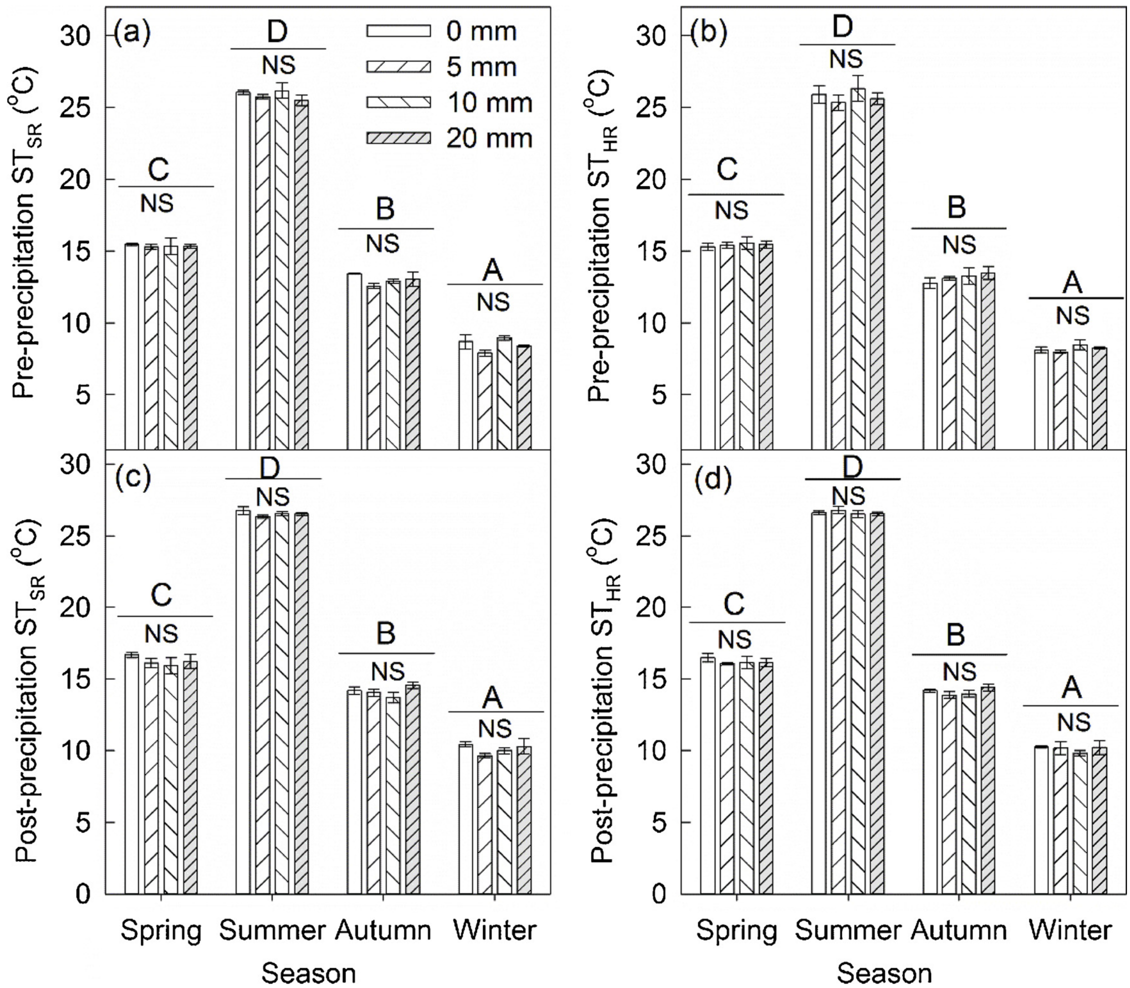

Fig. 1. Pre-precipitation soil temperature (a and b) and post-precipitation soil temperature (c and d) of the subplots for soil respiration (ST_{SR}) and heterotrophic respiration (ST_{HR}) under four precipitation levels in different seasons. Bars labeled with different uppercase letters indicate the significant differences among different seasons ($P < 0.05$). NS represents no significance among different precipitation events in each season ($P > 0.05$).

summer (both $P < 0.05$, Fig. 4). However, no significant differences were found between 10 and 20 mm precipitation events for the RS_{SR} and RS_{HR} in autumn and winter (both $P > 0.05$, Fig. 4).

3.7. Relative peak values of SR and HR

The relative peak values of SR and HR after precipitation pulse differed significantly between seasons (both $P < 0.01$, Table2). Relative peak values of SR and HR in spring were significantly higher than those in other seasons (all $P < 0.05$, Fig. 5). In addition, the responses of relative peak values for SR and HR to precipitation varied with seasons (both $P < 0.05$, Table 2). In spring and summer, the relative peak values of SR and HR under 20 mm events were significantly higher than that under 5 and 10 mm precipitation treatments (Fig. 5). In winter, however, precipitation events of 5 mm levels showed greater effects on the relative peak values of SR and HR compared with 10 and 20 mm events (Fig. 5).

3.8. Impacts of environmental factors on soil CO_2 efflux

Across 4 seasons and 4 precipitation events, post-precipitation ST, pre-precipitation SM, and SIN together explained 88.3% of the variance in SR, while 89.5% variation of HR could be accounted for by the TP, pre-precipitation SM, and MBC (Table 4). In spring, SIN (Partial R^2 = 0.339) and TP (Partial R^2 = 0.453) could explain 79.2% variation of SR ($P < 0.05$, Table 4), whereas 36.7% of the change in HR could be accounted for by BD (Partial R^2 = 0.367, $P < 0.05$, Table 4). In summer, post-precipitation SM and FRB together explained 75.5% of the variance in SR ($P < 0.05$, Table 4), whereas post-precipitation SM (Partial R^2 = 0.224, $P < 0.05$) and TP (Partial R^2 = 0.417, $P < 0.05$) were the best predictors of HR (Table 4). In autumn, MBC and FRB together explained 56.0% of the variances in SR, however, 85.0% of the changes in HR could be accounted for by pre-precipitation ST and MBC (Table 4). In winter, TP and post-precipitation ST were the best predictors of SR (R^2 = 67.4%), whereas BD, TP, and post-precipitation SM together explained 60.3% of the variance in HR (Table 4).

4. Discussion

4.1. Seasonal variations in the responses of SR to precipitation pulses

Our observation that SR showed substantial seasonal variations, with greater values in summer and lower values in winter, were consistent with numerous studies in forest ecosystems (Deng et al., 2013; Liu et al., 2019a; Luan et al., 2011a; Shabaga et al., 2015). The seasonal fluctuation of SR has long been attributed to the periodic changes in soil temperature (Carey et al., 2016; Lang et al., 2017), which could also be used to explain the variation of SR in this study due to its similar seasonal patterns with soil temperature (Figs. 1 and 3). The magnitude of SR in this study (0.43–4.20 g C m^{-2}) is comparable with that found in previous studies in the temperate forest (Bowden et al., 1993; Luan et al., 2011a).

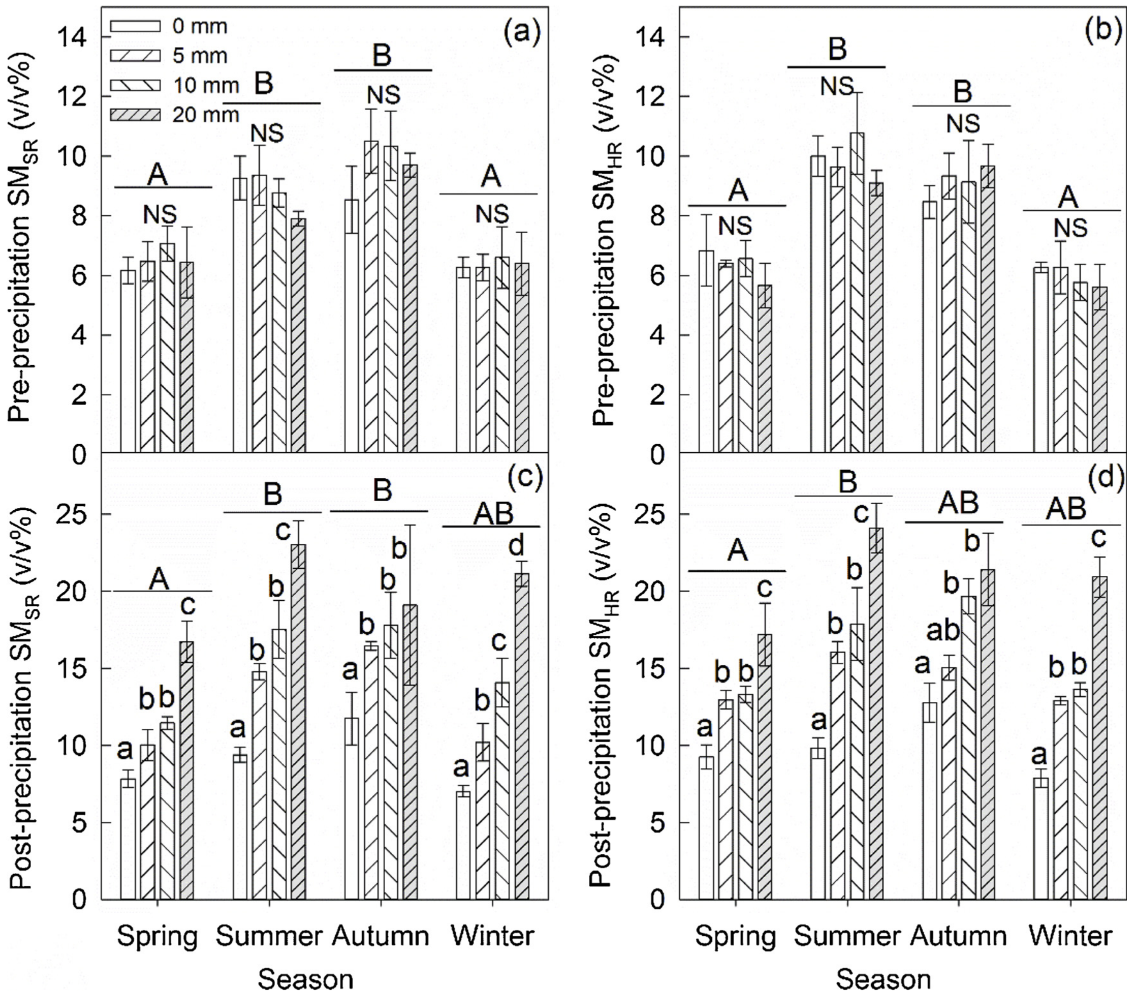

Fig. 2. Pre-precipitation soil moisture (a and b) and post-precipitation soil moisture (c and d) of subplots for soil respiration (SM_{SR}) and heterotrophic respiration (SM_{HR}) under four precipitation levels in different seasons. Bars labeled with different lowercase and uppercase letters indicate the significant differences among different precipitation events and different seasons, respectively ($P < 0.05$). NS represents no significance among different precipitation events ($P > 0.05$).

Regardless of the differences between seasons, the finding that most of the precipitation events showed strong positive effects on SR was in accordance with water manipulation experiments conducted in arid and semiarid ecosystems (Cable and Huxman, 2004; Huxman et al., 2004a; Sponseller, 2007). In contrast, however, Wang et al. (2012) found that natural precipitation events depressed SR in a subtropical exotic pine plantation, which may be explained by the anaerobic environment induced by the high mean annual precipitation in subtropical regions (1469 mm).

In this study, spring and summer had lower increase rate in SR (22.0–23.5%) in response to precipitation events than that in autumn and winter (36.6–48.6%) across the 24-hour experimental period (Fig. 3a). These differential responses may be explained by the following two aspects. First, the lower ST in autumn and winter compared with spring and summer (Fig. 1a and b), may result in lower activities of the plant (Romero-Olivares et al., 2017), and thus lead to lower background values of SR (Fig. 3a). Second, fewer precipitation events in autumn and winter may increase the proportion of CO_2 accumulated in soil porosity (Table 4), which always shows a rapid response to precipitation pulse through physical replacement.

Contradictory to our observations, however, a study in the Saline Desert found that precipitation-induced increment of SR was greater in June (summer, DOY181, +188%) than September (autumn, DOY262, +132%) (Ma et al., 2012a). Another study in an oak/grass savanna showed that ecosystem respiration was triggered in dry spring and summer, but not in autumn and winter (Ma et al., 2012b). The differential response magnitudes of SR to precipitation pulse indicates that the influences of episodic precipitation events on soil CO_2 efflux vary with seasons even in the same ecosystem. In a Sonoran desert, the response of SR to precipitation pulse has been ascribed to the biotic activity rather than abiotic processes (Sponseller, 2007). In contrast, however, the seasonal variations of the precipitation-induced increase of SR in this study can be mainly attributed to the abiotic factors, such as post-precipitation ST, pre-precipitation SM, and SIN across all four seasons (Table 4). On one hand, the abiotic factors have a remarkable seasonal fluctuation and always show substantial changes after precipitation input, especially for SM and SIN. On the other hand, pre-precipitation SM, representing soil dryness, plays critical roles in affecting soil microbe and plant root activity (Ren et al., 2018), thus may indirectly regulate the response of SR to precipitation pulse.

Biotic and abiotic factors showed different influences on the response of SR to precipitation pulse among different seasons (Table 4). The responses of SR to precipitation pulse can be mainly attributed to abiotic factors like TP in spring and winter, whereas may be largely explained by the biotic traits, such as FRB and MBC in summer and autumn (Table 4). The finding that TP contributed more to the responses of SR suggests that the replaced CO_2 in soil pore spaces during the precipitation-free period may be the main source of triggered SR in spring and winter (Yan et al., 2014). As an important influencing factor, SM before precipitation pulse in spring and winter was lower than that in summer and autumn (Fig. 2a) due to the lower precipitation frequency, which could increase the proportion of gaseous phase in soil

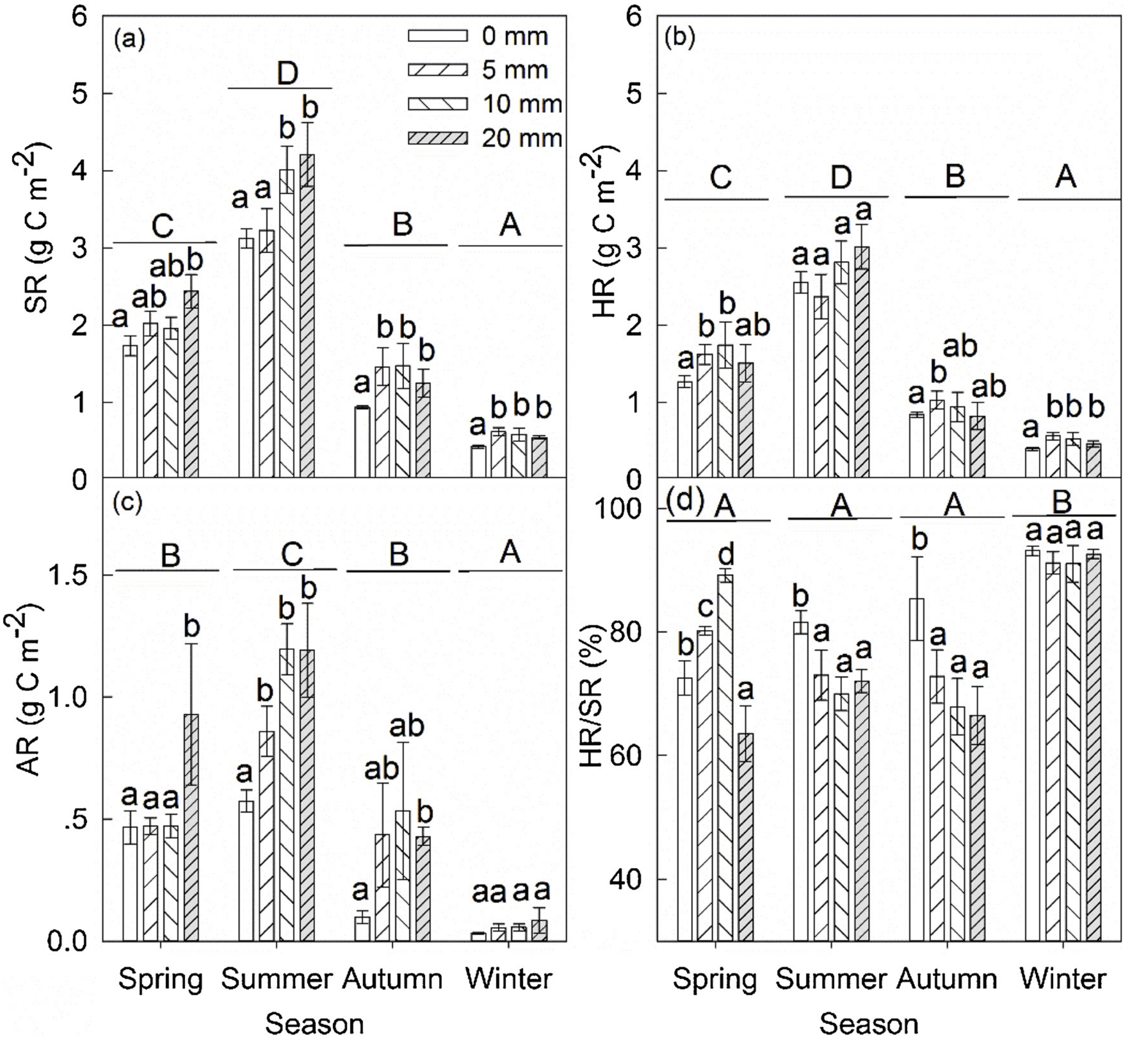

Fig. 3. Effects of precipitation pulse on soil respiration (SR), heterotrophic respiration (HR), autotrophic respiration (AR), and the proportion of HR in SR (HR/SR) during the experimental period (24 h) in each season. Bars labeled with different lowercase and uppercase letters indicate the significant differences among different precipitation events and different seasons, respectively ($P < 0.05$).

Table 3
Increases in seasonal cumulative soil CO_2 efflux (g C m^{-2}) of soil respiration (SC_{SR}), heterotrophic respiration (SC_{HR}), and autotrophic respiration (SC_{AR}) induced by different precipitation events [compared to the plots without precipitation addition (0 mm)] across 3 months. Values in parenthesis are the proportion (%) of precipitation-induced increase in seasonal cumulative CO_2 efflux in annual total soil CO_2 efflux.

Type	Precipitation event (mm)	Spring	Summer	Autumn	Winter	Total
SC_{SR}	5	7.44(1.3)	1.71(0.3)	8.94(1.6)	2.78(0.5)	20.86(3.6)
	10	4.59(0.8)	6.09(1.1)	3.48(0.6)	0.81(0.1)	14.98(2.6)
	20	6.70(1.2)	10.07(1.7)	1.15(0.2)	0.11(0.02)	18.03(3.1)
	Sum	18.73(3.3)	17.86(3.1)	13.57(2.4)	3.71(0.6)	53.87(9.4)
SC_{HR}	5	5.44(1.2)	0.81(0.2)	3.20(0.7)	2.44(0.5)	11.88(2.5)
	10	3.35(0.7)	1.79(0.4)	0.65(0.1)	0.68(0.1)	6.47(1.4)
	20	1.27(0.3)	4.30(0.9)	0.92(0.2)	0.06(0.1)	6.56(1.5)
	Sum	10.06(2.1)	6.91(1.5)	4.77(1.0)	3.18(0.7)	24.91(5.3)
SC_{AR}	5	2.00(1.9)	0.90(0.9)	5.74(5.4)	0.34(0.3)	8.98(8.5)
	10	1.24(1.2)	4.29(4.1)	2.84(2.7)	0.13(0.1)	8.50(8.0)
	20	5.43(5.1)	5.76(5.5)	0.23(0.2)	0.05(0.1)	11.47(11.0)
	Sum	8.67(8.2)	10.96(10.4)	8.81(8.3)	0.53(0.5)	28.96(27.5)

pore spaces and improve the diffusion of gases. Compared with spring and winter, precipitation events induced a greater increase in SM in summer and autumn, probably due to higher antecedent SM (Fig. 2). Therefore, the increased soil water availability after precipitation events can lead to microbial cell lysis or the rapid mineralization of cytoplasmic solutes and release the mineralized product into the surrounding environment to dispose of its osmolytes, which have accumulated during the dry period (Schimel et al., 2007). Moreover, the greater SM means more water percolated to the rhizosphere and triggers root activity, thus increased autotrophic respiration (Huxman

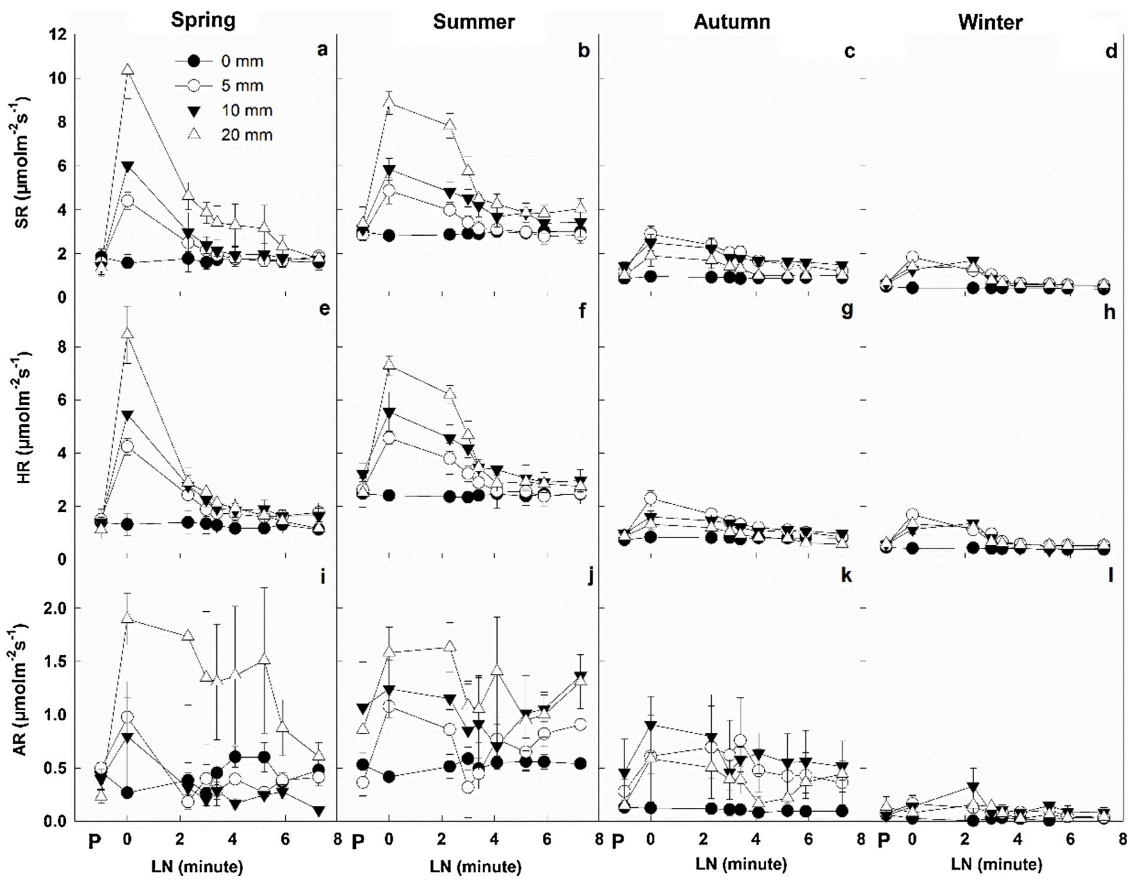

Fig. A1. Time courses of soil respiration (SR; a, b, c, and d), heterotrophic respiration (HR; e, f, g, and h), and autotrophic respiration (AR; i, j, k, and l) as affected by different precipitation events in different seasons (a, e, and i for spring; b, f, and j for summer; c, g, and k for autumn; d, h, and l for winter). We used a linear scale for the y-axis and a logarithmic scale for the x-axis to make the illustration more readable. Mean ± *SE*., $n = 3$.

et al., 2004b). The elevated SM may have "chronic" impacts on the continuous release of root exudates (Phillips et al., 2011), which is strongly related to plant photosynthetic activity (Mitra et al., 2016).

4.2. Responses of HR and AR to precipitation pulses

Similar to SR, both HR and AR also showed substantial temporal variations, with greater values in summer (Fig. 3b and 3c), which was consistent with previous studies (Liu et al., 2016; Luan et al., 2011a). In accordance with the explanation in previous field experiments (Fang et al., 2018; Luan et al., 2012), we also attributed this to the temporal fluctuation of soil temperature.

Across all four seasons, the seasonal variations of the response of HR to precipitation pulse can be ascribed to both abiotic (TP and pre-

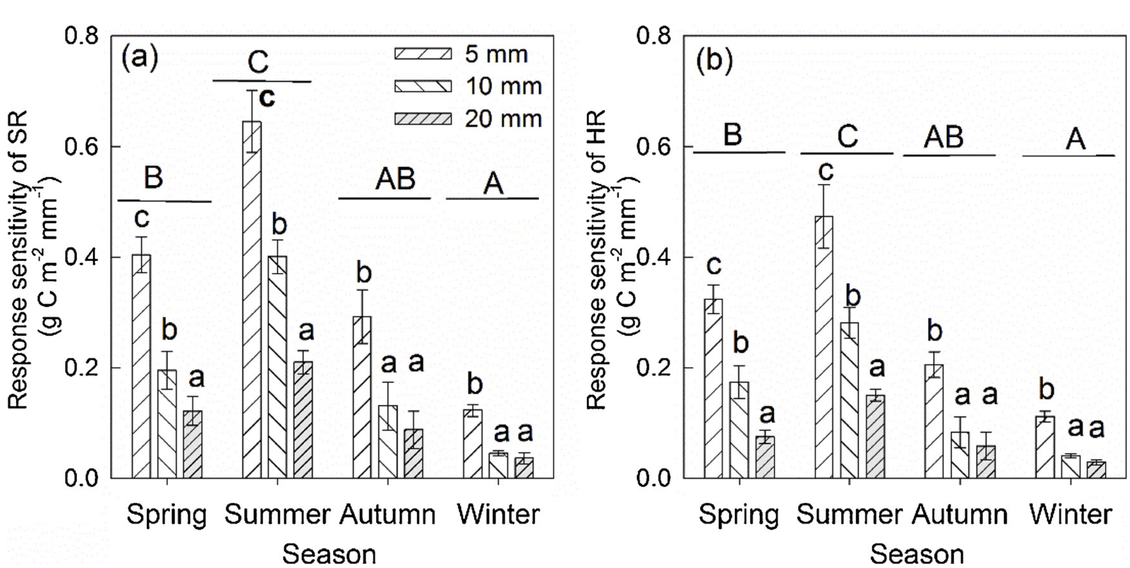

Fig. 4. Response sensitivity of soil respiration (SR) and heterotrophic respiration (HR) to precipitation pulse in different seasons. Bars labeled with different lowercase and uppercase letters indicate the significant differences among different precipitation events and seasons ($P < 0.05$).

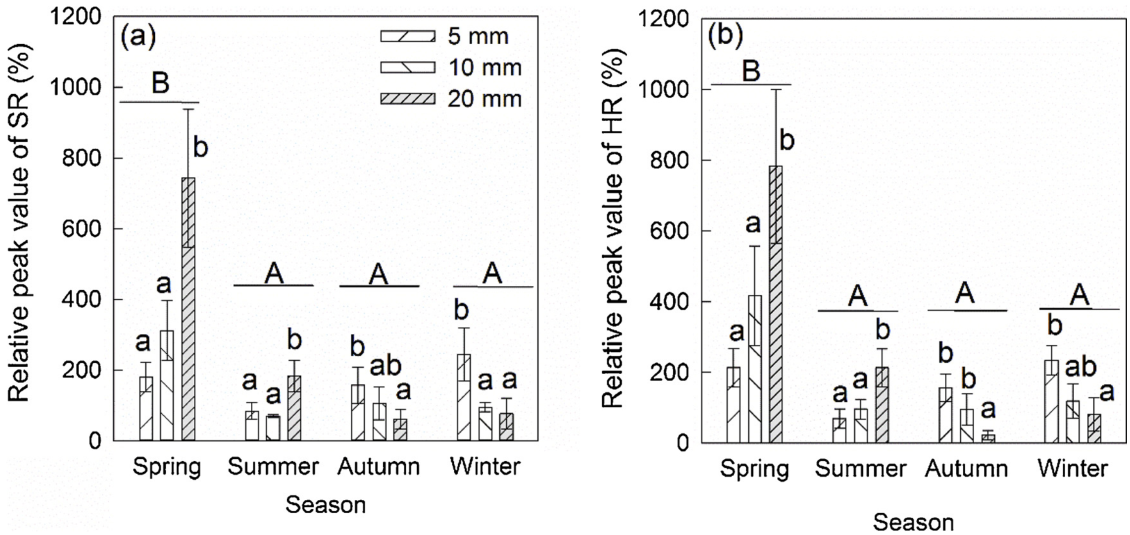

Fig. 5. Relative peak values (%) of soil respiration (SR) and heterotrophic respiration (HR) affected by precipitation pulse in different seasons [*e. g.* (SR_{peak}-$SR_{pre-precipitation}$)/$SR_{pre-precipitation}$ × 100]. Bars labeled with different lowercase and uppercase letters indicate the significant differences among different precipitation treatments and seasons ($P < 0.05$).

Table 4
Summary of stepwise multiple regression showing dependences of soil respiration (SR) and heterotrophic respiration (HR) after precipitation pulse across the experimental period (24 h) on environmental factors. SIN, soil inorganic nitrogen; TP, total soil porosity; PoSM, post-precipitation soil moisture; FRB, fine root biomass; MBC, microbial biomass carbon; PoST, post-precipitation soil temperature; PrSM, pre-precipitation soil moisture; BD, bulk density; PrST, pre-precipitation soil temperature.

Dependent variable	Season	Independent variables	Partial R^2	Adjusted R^2	P value
SR	Spring	SIN	0.339	0.339	0.028
		TP	0.453	0.792	0.001
	Summer	PoSM	0.280	0.280	0.045
		FRB	0.475	0.755	0.001
	Autumn	MBC	0.447	0.447	0.010
		FRB	0.113	0.560	0.012
	Winter	TP	0.445	0.445	0.011
		PoST	0.229	0.674	0.003
	All seasons	PoST	0.437	0.437	0.001
		PrSM	0.224	0.661	0.001
		SIN	0.222	0.883	0.001
HR	Spring	BD	0.367	0.367	0.022
	Summer	PoSM	0.224	0.224	0.048
		TP	0.417	0.641	0.004
	Autumn	PrST	0.746	0.746	0.003
		MBC	0.104	0.850	0.001
	Winter	BD	0.259	0.259	0.052
		TP	0.198	0.457	0.026
		PoSM	0.146	0.603	0.002
	All seasons	TP	0.356	0.356	0.001
		PrSM	0.225	0.581	0.001
		MBC	0.314	0.895	0.001

precipitation SM) and biotic factors (MBC). It has been reported that TP changes over the short term due to the influence of wetting-drying cycles as well as during vegetative and seasonal cycles (Mora and Lázaro, 2014). Our finding suggests that the physical displacement of CO_2 from soil pore spaces following precipitation pulses may be the main source of HR, due to the higher contribution of TP to the HR (35.6%, Table 4). Moreover, the elevated soil microbial activity, probably due to the improved soil water availability following precipitation events, may also partly contribute to the increased HR (Table 4).

Inconsistent with the response of SR to precipitation events, however, HR showed higher positive responses in spring and winter, with neutral response in summer (Fig. 3b). The finding indicates that the increased SR induced by precipitation pulse in the growing season (summer), especially under 10 and 20 mm levels, may largely originate from AR (Fig. 3c). Contradictory to our observation, however, Fan et al. (2015) found that HR contributed to approximately 50% of SR in the sub-canopy in the growing season. The elevated HR after precipitation pulse in both spring and winter may be attributed to the BD, which closely associated with spring root development and winter freezing-thawing alteration (Bruand et al., 1996).

In contrast to the influences of precipitation pulses on HR, AR was substantially elevated by all precipitation events in summer. First, the oak species associated with ectomycorrhizal fungi may produce greater root exudation and labile C substrate in summer compared with other seasons (Yin et al., 2014). Second, the shallow, sandy loam soils and hilly topography in the study region are not optimal for moisture retention. The water applied to the untrenched-plots may infiltrate to the deeper rooting zone and stimulate root growth and turnover, thus elevate AR.

4.3. Responses of the proportion of HR in SR to precipitation pulses

In the control plots, the values of HR/SR varied from 66.5%–93.1%, which is comparable to previous studies in the temperate oak forest (Liu et al., 2014; Luan et al., 2011b). Since only a few studies have quantified the values of HR/SR under precipitation pulses, it is difficult to compare our results to those in other forest ecosystems. A study in Mediterranean ecosystems found that the increased SR was primarily due to the enhancement of HR, probably due to the degradation of easily decomposable substrates (Inglima et al., 2009). On the contrary, however, we found that the values of HR/SR following precipitation pulses were significantly reduced in both summer and autumn (Fig. 3d). These may be attributed to the difference in ecosystem types, soil physical-chemical characteristics, and degree of dryness. As Cable et al. (2008) reported that soil texture drives differences in the effects of pulses on the magnitude and the sensitivity of HR and AR. Similar to the above statement, the water added to plots may easily percolate to the deeper root zone in summer and autumn due to the shallow and sandy property of the soils. Thus, it may trigger greater root/rhizosphere respiration (Table 3) and reduce the values of HR/SR.

4.4. Effects of precipitation pulse on the response sensitivities of SR and HR

Our observations that both RS_{SR} and RS_{HR} showed the highest values in summer and the lowest ones in winter (Fig. 4) suggests that the increments of SR and HR caused by per unit of precipitation varied with seasons. The magnitudes of water applied to plots were equivalent among different seasons. Therefore, the seasonal differences in the RS_{SR} and RS_{HR} were mainly resulted from the variations of SR and HR among different seasons. The greater values of SR and HR in summer (Fig. 3a, b) linked with vigorous plant and microbe activity, would be responsible for the higher RS_{SR} and RS_{HR} in summer. In addition, the finding that RS_{SR} and RS_{HR} decreased with the increased precipitation size indicates that SR and HR showed larger RS under smaller precipitation event. The differences in RS between precipitation events may result from the following two aspects. First, the increment of SR and HR after precipitation pulses decreased with elevated precipitation events, probably due to the reduced soil permeability (Deng et al., 2011). Second, higher precipitation events (10 and 20 mm) may induce a greater leaching rate of dissolved organic C, thus decrease substrate availability and the increments in SR and HR (Knapp et al., 2008).

5. Conclusions

By simulating episodic precipitation events with different intensities, our study showed that substantial seasonal variations in soil CO_2 efflux in response to precipitation pulses in a temperate oak forest in Central China. The estimated total soil CO_2 efflux through SR caused by precipitation events was greater in summer and autumn than that in spring and winter. Precipitation pulse significantly elevated HR in winter and stimulated AR in summer. The seasonal differences in the responses of soil CO_2 efflux to precipitation pulses primarily depend on the different contributions of biotic and abiotic factors. This study brings new and valuable information for our general understanding of the seasonal variations in the response of soil CO_2 efflux to precipitation events and biotic/abiotic determinants of the process in forest ecosystems. Our study indicates that seasonal variations in the response of soil CO_2 efflux to precipitation events should be highlighted while estimating the Birch effect and its role in terrestrial C cycling.

Acknowledgments

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